



TITLE:

Japanese monkeys (*Macaca fuscata*) spontaneously associate alarm calls with snakes appearing in the left visual field.

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CITATION:

Shibasaki, Masahiro ...[et al]. Japanese monkeys (*Macaca fuscata*) spontaneously associate alarm calls with snakes appearing in the left visual field.. *Journal of comparative psychology* 2014, 128(3): 332-335

ISSUE DATE:

2014-08

URL:

<http://hdl.handle.net/2433/189546>

RIGHT:

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- 1 Running Head: Spontaneous association between alarm calls and snakes in monkeys
- 2
- 3 Short communications to Journal of Comparative Psychology
- 4
- 5 Japanese monkeys (*Macaca fuscata*) spontaneously associate alarm calls with snakes appearing in
- 6 the left visual field
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8

## Abstract

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Many socially living animals are sensitive to a potential predator as part of their anti-predator strategy. Alarm calls function to deter predators and to help other group members detect danger. The left visual field is involved in detection of potential threats or predators in many vertebrates, but it is unclear how alarm calls influence visual detection of a potential predator. Here, we experimentally examined how alarm calls spontaneously influence the search for pictures of a potential predator in captive Japanese macaques. We used an audiovisual preferential-looking paradigm by presenting pictures of a snake and a flower simultaneous with either a recording of alarm calls or contact calls. We found no difference in gaze duration between the two picture types when playing back contact calls. Monkeys looked significantly longer at pictures of snakes than at those of flowers when alarm calls were played back if the snake pictures were presented on the left side of the monkey's visual field, indicating right hemispheric bias during processing of predator representations. This is the first laboratory demonstration of auditory enhancement of visual detection of predators in the left visual field in animals, which will contribute to a better understanding of alarm call studies conducted in the wild.

*Keywords:* anti-predator strategy; visual lateralization; alarm call; snake fear; nonhuman primates

24 Human and nonhuman primates appear extremely sensitive to biologically threatening stimuli  
25 such as snakes (LoBue, Rakison, & DeLoache, 2010). Humans are easily conditioned to react to  
26 pictures of snakes, and this conditioned fear of snakes is resistant to extinction (see Ohman &  
27 Mineka, 2001, 2003 for a review). Similar to humans, laboratory-reared rhesus monkeys are  
28 quickly conditioned to fear snakes after watching videotapes of monkeys being frightened by  
29 snakes (Cook & Mineka, 1990). Humans and nonhuman primates also detect snakes faster than they  
30 detect neutral stimuli (e.g., flowers) during visual search tasks (LoBue et al., 2010). Even young  
31 children and lab-reared monkeys with no experience with snakes are faster to detect snakes than  
32 flowers (LoBue & DeLoache, 2008; Shibasaki & Kawai, 2009).

33 Visual lateralization has been revealed during visual processing of threatening stimuli in  
34 primates and many other vertebrates (see Rogers & Andrew, 2002; Rogers, Vallortigara, & Andrew,  
35 2013 for reviews). Horses react more strongly to a frightening stimulus when it is presented in the  
36 left visual field (Austin & Rogers, 2007), and horses use the left eye to view a potential threat or  
37 predator (Farmer, Krueger, & Byrne, 2010). The stripe-faced dunnart showed the higher reactivity  
38 when the subjects were presented with a model snake on their left side (Lippolis, Westman,  
39 McAllan, & Rogers, 2005), thus indicating specialization of the right side of the brain in controlling  
40 the escape response, as found previously in toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002).  
41 Gelada baboons direct more aggressive responses to conspecifics on their left side than they do to  
42 those on their right side (Casperd & Dunbar, 1996). The left visual field bias likely reflects right  
43 hemisphere dominance during visual processing of emotional information (Rogers et al., 2013).

44 Similar to the visual system, specialized cognitive processing has evolved during auditory  
45 communication in many animals. Many socially living animals produce predator-specific alarm  
46 calls as part of their anti-predator strategy (Zuberbuhler, 2003 for review). Alarm calls convey

representation of potential predators and further evoke animal escapes. Despite clear evidences for association of predator presence and alarm calls, it has been unclear how alarm calls influence detections of potential predators. For the learning of alarm calls, experiences like observing demonstrators would be necessary for nonhuman primates (e.g., Campbell & Snowden, 2009).

The aim of this study was to investigate how alarm calls spontaneously influence detection of potential predator pictures by captive Japanese macaques, particularly if they are presented in the left visual field. We assessed this with an audiovisual preferential-looking paradigm in which Japanese macaques were simultaneously presented with alarm calls and pictures of a predator. Audiovisual preferential-looking paradigms have been used to investigate matching ability in the auditory and visual sense modalities in animals (Ghazanfar & Logothetis, 2003) and human infants (Kuhl & Meltzoff, 1982). In a typical task, pairs of images (or movies) are presented to subjects in conjunction with an auditory stimulus. The rationale is that if the auditory stimulus has the power to evoke recall of an associated mental representation or emotion, then subjects are expected to look longer at the matching visual stimulus relative to a control stimulus.

In our experiments, we paired pictures of snakes and flowers with the Japanese macaques' alarm and contact calls. If alarm calls emotionally enhance visual detection of a potential predator, biased visual detection of threatening stimuli would occur more clearly.

## Method

*Subjects.* We used 16 female Japanese macaques (*Macaca fuscata*) aged 2–6 years. All were born into social groups housed in outdoor enclosures at the Primate Research Institute, Kyoto University and naïve to seeing snakes.

*Apparatus.* Subjects were tested in a custom-made experimental box (450 mm W × 450 D ×

600 H) that was positioned in a sound attenuating chamber (RE-246, TRACOUSTICS). Three sides of the experimental box were covered with transparent polycarbonate boards, and the other was the cage gate. Subjects were tested individually in the experimental box using a 22-inch LCD screen (ProLite E2208HDS, IIYAMA, Tokyo, Japan) mounted on the experimental box, which enabled subjects to look at the monitor. The screen was connected to a computer placed outside the sound chamber for stimulus presentation. The screen resolution was set to  $1600 \times 800$  pixels. A small 8.5-mm 1-in -pinhole infrared-sensitive CCD camera ( $40 \times 25 \times 36$  mm, ITC-401, ITC, Tokyo, Japan) placed at the center of the monitor was connected to a TV screen (LC-22K5, SHARP, Japan) outside the sound chamber for gaze analysis and to a video camera (GZ-MG840-A, Victor, Japan) to record the subject's behavior during experiments. An active speaker (SRS-Z100, Sony, Tokyo, Japan) placed under the center of the LCD screen was used to deliver the playback stimuli.

*Visual Stimuli.* We used two snake and two flower pictures as visual stimuli. The pictures, which were available from the internet (<http://www.pitt.edu/~mcs2/herp/SoNA.html>, [http://www.flowerpictures.net/flower\\_pictures.htm](http://www.flowerpictures.net/flower_pictures.htm)), and used in previous studies (Shibasaki & Kawai, 2009). The pictures were reformatted to  $300 \times 400$  pixels. The snakes used for stimuli were species which wild Japanese macaques never naturally see in the forest in order to neglect the possible effect of “innate” reactions to specific snake species which wild macaques can see. The average luminance and contrast were equalized across all stimuli with Adobe Photoshop CS5.

*Auditory Stimuli.* We used an alarm call and a contact call series as auditory stimuli (see online supplementary Figure S1). Both calls were recorded from free-ranging Japanese macaques by HK in 2006. Alarm calls of Japanese macaques were defined as being of only a single type given to dogs, snakes and other potential predators (Green 1975). Contact calls are frequently exchanged among group members during the movement to maintain their cohesion (Koda, 2004). Both

93 playback stimuli consisted of a series of three calls delivered at the same rate over a total duration of  
94 10 s. Calls were edited to match the maximum intensities between calls using Adobe Audition 2.0.

95 *Procedure.* Prior to each trial, we displayed a fixation cross in the center of the screen to draw  
96 the monkeys' attention. Once this occurred, the experimenter simultaneously displayed pictures of a  
97 snake and a flower on the screen. The distance between the left and right image centers was 394.9  
98 mm. Presentation time was 10 s. We simultaneously broadcasted one auditory stimulus as a 10-s  
99 series consisting of either three alarm or three contact calls. The trial was performed once in a day  
100 for each subject. Two trials per subject were performed for each call, counterbalancing the side  
101 positions of paired stimuli. Consequently four trials were performed for each subject monkey.

102 *Video Analysis.* We measured the total looking duration for both images during the 10-s trial.  
103 We categorized subjects' gaze directions as 1) looking to the left side of the screen, 2) looking to the  
104 right side of the screen, and 3) not looking at the screen. Coding was carried out by an observer who  
105 was unfamiliar with the aims of this study. Coding units consisted of 33-ms-long video frames  
106 extracted with custom-made software. The procedure was the same as with our previous study using  
107 visual paired comparison tasks (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012)

108 *Statistical Analysis.* We performed a three-way repeated-measures analysis of variance  
109 (ANOVA) using Statistica 6.1 (StatSoft Japan, Inc. Tokyo, Japan) to examine the effects of call  
110 type (alarm vs. contact call), stimulus type (snake vs. flower), and position (left vs. right). If  
111 interaction effects were found, we also performed post-hoc pairwise comparisons using Tukey's  
112 honestly significant difference test. Significance levels were all set to  $p < .05$ .

113 *Ethical Note.* All procedures were approved by the ethics committee of Primate Research  
114 Institute of Kyoto University (permit number 2011-070) and were in accordance with the Guide for  
115 the Care and Use of Laboratory Primates (Third Edition of Primate Research Institute, Kyoto

University).

## Results

Prior to analysis, we performed Levene test to check the normal distribution of the data, and confirmed that our data were normally distributed,  $p > 0.13$ . The repeated-measures ANOVA revealed a significant main effect of stimulus type,  $F(1, 30) = 10.13$ ,  $p < .005$ ,  $\eta_p^2 = .25$ , but not of call type,  $F(1, 30) = 1.01$ ,  $p = .32$ ,  $\eta_p^2 = .03$ , and position,  $F(1, 30) = 3.14$ ,  $p = .09$ ,  $\eta_p^2 = .09$ . More importantly, a three-way interaction effect was found in looking time (LT),  $F(1, 30) = 4.70$ ,  $p < .05$ ,  $\eta_p^2 = .14$ . To examine how three main effects interacted with each other, post-hoc comparisons were performed. The post-hoc analyses further revealed that this was due to a significant difference in looking time between the snake and flower pictures in the alarm condition (mean LT  $\pm$  95% confidence interval, snake:  $52.50 \pm 15.37$  frames; flower:  $21.44 \pm 10.71$  frames,  $p = .02$ , Figure 1), but not in the contact-call condition (snake:  $39.50 \pm 16.93$  frames; flower:  $23.69 \pm 8.93$  frames,  $p = .65$ , Figure 1), when snake pictures were presented on the left, indicating that monkeys looked significantly longer at pictures of snakes when they heard alarm calls and the snake picture was presented in the left visual field. In contrast with the condition where the snake picture appears on the left side, there is no significant difference in looking time between the snake and flower pictures in both the alarm condition (snake:  $37.75 \pm 12.44$  frames; flower:  $40.81 \pm 12.32$  frames,  $p = .99$ , Figure 1) and the contact-call condition (snake:  $64.69 \pm 20.36$  frames; flower:  $44.69 \pm 14.50$  frames,  $p = .36$ , Figure 1), when snake picture was presented on the right side.

## Discussion

Our results are the first laboratory-based demonstration in nonhuman animals that predator



139 alarm calls enhance looking at predator images. Subjects looked longer at pictures of snakes when  
140 they heard alarm calls compared with when they heard contact calls, suggesting specialized  
141 cognitive traits for audio-visual processing of fear related stimuli. This would agree with the notion  
142 that the amygdala responds audio-visually to fear related stimuli (Kuraoka & Nakamura,  
143 2007). Furthermore, our study showed left-side bias during snake picture processing under the alarm  
144 call condition, suggesting right-hemispheric neural bias. Right-hemisphere dominance in amygdala  
145 processing has also been found in humans during processing of fear-relevant stimuli such as angry  
146 human faces (Gainotti, 2012). Equally relevant studies have found a left-eye bias in response to  
147 frightening stimuli in vertebrates, including fish, frogs, lizards, birds, rodents, dogs, horses, and  
148 primates (Kaplan & Rogers, 2013; Vallortigara & Rogers, 2005 for review). Particularly, recent  
149 studies in dogs have revealed the biased monitoring reactions to social stimuli. The experiment  
150 using a head-orienting procedure showed that dogs turned their head to the right side (left  
151 hemisphere) in response to conspecific vocalizations, but to the left side in response to the sound of  
152 the thunderstorm (Siniscalchi, Quaranta, & Rogers, 2008). Dogs turned preferentially their head to  
153 the left side in response to the silhouettes of snakes (Siniscalchi, Sasso, Pepe, Vallortigara, &  
154 Quaranta, 2010). The two studies suggests dog's biased processing in right hemisphere for  
155 audio-visual fear related stimuli. The similar right hemisphere dominance has been found in  
156 primates. The common marmosets displayed right-eye preferences for viewing a piece of preferred  
157 food (Hook-Costigan & Rogers, 1998). However, when the marmosets viewed a model snake, they  
158 displayed increased arousal and the eye preferences shifted away from a preference for the right eye  
159 to a left-eye preference (Hook-Costigan & Rogers, 1998). Our findings are in line with these  
160 previous findings, suggesting a hemispheric bias in the neural mechanisms of emotional processing,  
161 particularly fear processing.

Snake fear in humans and nonhuman primates is often discussed in terms of underlying learning processes. Pioneer studies in macaques and squirrel monkeys have found that fear of snakes is selectively and rapidly learned, suggesting a biological preparedness for conditioning of snake fear (Mineka, Davidson, Cook, & Keir, 1984). According to this “preparedness theory” (Seligman, 1971), some natural stimuli are easier to condition to fearful responses than others, suggesting that animals are evolutionarily prepared to learn some associations more rapidly and effectively than others. Experiments with laboratory-reared monkeys naive to snakes have shown that they rapidly acquire a fear of snakes by observing other monkeys showing fear responses to snakes (Mineka & Öhman, 2002). Such learning is strong and persistent (Cook, Mineka, Wolkenstein, & Laitsch, 1985; Mineka et al., 1984), even if the fearful model monkey is shown on video (Cook & Mineka, 1990). Of particular importance is that our subjects reared in captivity were naive to snakes. In conclusion, monkeys appear to have an innate sensitivity to snakes, and alarm calls appear to be particularly suited to this process.

We showed spontaneous lateralized looking at a predator evoked by alarm calls in monkeys, suggesting audiovisual correspondence during processing of emotional stimuli, demonstrated by the association between predator images and alarm calls. Here we hypothesize that learning a fear of snakes requires experience, whereas the association between alarm calls and potential predators is innate. However, we should acknowledge some research limitations of limited set of stimuli used here. The further study with a large number of stimulus sets would be necessary to generalize our findings. Furthermore, we need to compare the snake pictures to other pictures instead of flowers and replicate our findings to reject the possibility that the results might just be based on the lack of preference for snakes when presented on the right side with alarm call.

185 *Acknowledgements*

186       We thank Akemi Kato, Takumi Kunieda, Anna Sato, and Keiko Ishida for looking after the  
187 monkeys, and for help with data acquisition and coding. We are grateful to Klaus Zuberbuhler for  
188 his comments on our studies. This study was supported by JSPS Grant-in-Aids for Scientific  
189 Research (B, #22330200, #25285199) to Nobuyuki Kawai (HK joined as co-PI), a JSPS fellowship  
190 (#23.5358) to MS, and the Young Researcher Overseas Visit Program of Kyoto University.

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264 Figure legend

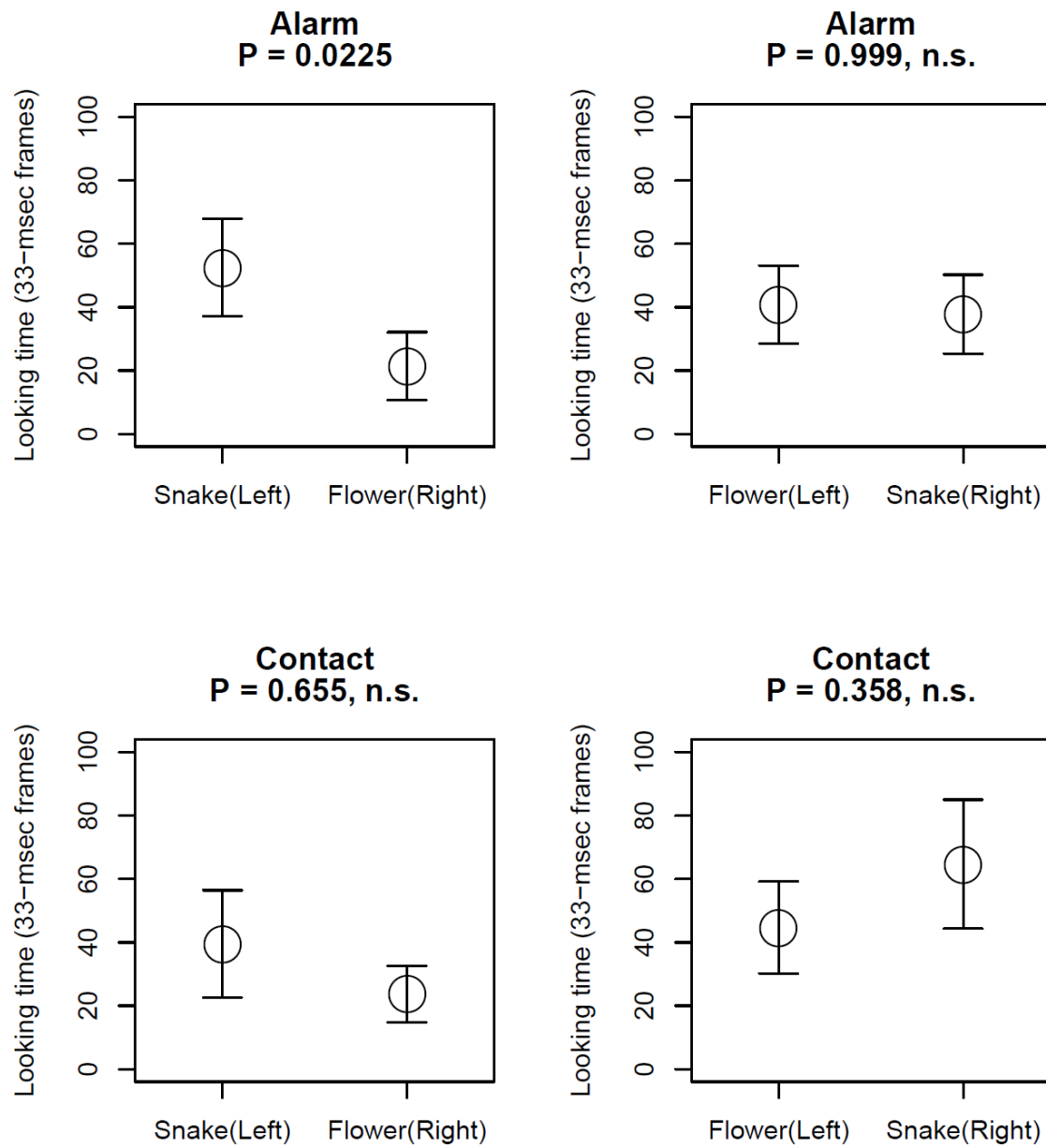
265 Figure 1. Looking duration of Japanese macaques at images of snakes and flowers presented to the  
266 left or right visual field while hearing recordings of conspecific alarm calls or contact calls (means  
267  $\pm 95\%$  confidence intervals)

268 Online Supplementary Figure legend

Figure S1. Sound spectrogram of calls used for stimuli in the experiments.



Figure 1



Online supplementary material

Figure S1

